

Trapezia and *Tetralia* (Decapoda, Brachyura, Xanthidae) as Obligate Ectoparasites of Pocilloporid and Acroporid Corals^{1, 2}

JENS W. KNUDSEN³

THE OCCURRENCE of marine invertebrates in the branches of living and dead corals has long been recognized. Two crab genera, *Trapezia* and *Tetralia*, of the family Xanthidae are determined by Garth (1964) as being obligate commensals of the coral families Pocilloporidae and Acroporidae, respectively. Crane (1947) lists species of the genus *Trapezia* as being found only in pocilloporid corals along the west coast of tropical America. Miyake (1939), in listing the Brachyura of Micronesia, records *Trapezia cymodoce* as collected from *Stylophora*, a pocilloporid coral. Garth's original collecting techniques used at Eniwetok Atoll, Marshall Islands, were refined in his later collecting in July 1959, at which time he segregated each collection of coral by species to avoid mixing coral commensals found therein.

From 10 collections of acroporid coral Garth extracted two species of *Tetralia* (*T. glaberrima*, also taken once on *Pocillopora damicornis*, and *T. heterodactyla*), but found no specimens of *Trapezia*. Conversely, from 14 collections of pocilloporid corals he obtained five species of *Trapezia* (*cymodoce*, f. *ferruginea*, *digitalis*, *danai*, *rufopunctata*), but obtained only one specimen of *Tetralia*. Because of this rather exclusive distribution of the species of *Trapezia* and *Tetralia*, Garth rightly concludes that these are obligate commensals of long standing. Garth states (1964:142), "In general, the larger forms were found in the more robust Pocilloporidae, the smaller forms in the more delicate Acroporidae. Thus, the *Trapezia* species occurred in the pocilloporid corals, the *Tetralia* species in the acroporid corals, although *Tetralia*

was found once in *Seriatopora*, a finely branching member of the Pocilloporidae in which the spatial relationships found in the Acroporidae obtain." Thus Garth suggests a basis of crab size and coral spatial relationships as a possible basis of this "obligatory commensalism."

The writer spent four months at the Eniwetok Marine Biological Laboratory, from February through May 1965, in order to work on crab ecology and to determine the possible basis for this seemingly ironclad crab-coral relationship. Several possible theories seemed worth investigating in order to ascertain the factors upon which this commensal-host relationship is maintained: (1) the crab-size coral-space relationship suggested by Garth; (2) that some oceanographic condition (water temperature, currents, wave action, etc.) is coincidentally required by both the crab genus and its respective host coral, therefore making the relationship one of convenience; (3) that the crab genera may prove to be filter-feeders utilizing the same food required by their host corals, thus making the relationship one of simple convenience; (4) that the host corals provide some special form of protection, in addition to simple hiding places, which exclusively attract the crab genera; (5) the possibility that more collections would reveal that both genera of crabs would be found almost equally on the Pocilloporidae and Acroporidae.

These five suppositions served to initiate field research. The first three (space-size, oceanography, food requirements) could be the key to the coral-crab relationship either with live or dead corals of the proper families, providing such corals were not overgrown with algae. However, supposition number four (special protection) could function only with live corals. Garth's term of obligate commensal was defined for our work as a situation where the crabs in question are obligated to live with their host corals in order to receive some benefit which

¹ Sponsored by NSF Grant G-2412.

² Facilities and sponsorship at the Eniwetok Marine Biological Laboratory by the Atomic Energy Commission.

³ Pacific Lutheran University, Tacoma, Washington. Manuscript received March 21, 1966.

they could not otherwise obtain, but are not harmful to their coral hosts.

Crane (1947:83) and Garth (1964:142) note that *Trapezia* and/or *Tetralia* are limited in number to a single mated pair (with their young, Garth adds) on smaller coral heads, establishing a territory which they somehow protect (Garth). It must be noted, however, that the crabs have normal pelagic larvae, the megalops of which must seek out the proper species of host coral before settling and undergoing metamorphosis. Thus, hundreds of corals must be rejected by each megalops until the proper species is found. Gurney (1938:76-77) described the zoal stages of *Trapezia cymodoce* and *Tetralia glaberrima* which he reared from adults in captivity, but made no note of the larvae being photonegative. Thus, one may assume that normal photopositive larvae would be attracted away from the coral host of the adult crab, to take up a normal pelagic existence. Furthermore, of the 306 clutches of eggs that we hatched out at the Eniwetok laboratory, 22 belonged to species of *Trapezia* and *Tetralia*. All of their larvae proved to be photopositive, thus indicating that they are pelagic in their larval development.

To test the supposition that size-space, oceanographic, or food relationships may serve as a key factor in commensalism, Experiment No. 1 was conducted in a deep pool on the ocean side of the north end of Eniwetok Island. Pocilloporid and acroporid corals attached to large but movable rocks were collected and killed by air drying. Some of these corals were dried for three days while others were cleaned by rotting the tissue, washing, soaking out, and then air drying. Next, these corals were tagged, restocked with newly collected crabs (*Trapezia* on pocilloporid coral and *Tetralia* on acroporid coral, the normal hosts), and placed in the bottom of the pool. Controls consisted of tagged live corals which were stocked with newly collected crabs of the proper species.

After three days it was observed that all of the experimental crabs were missing from the dead corals (though some galatheid crabs had taken up residence). All crabs on the control corals were present (even when rechecked several weeks later). This suggested that either live coral or coral with the natural color (as

opposed to the white color of dead coral) is required for protection.

To test the premise that coral color may be an important factor (Experiment No. 2), new corals were killed, cleaned, washed, dyed with vital stains of an appropriate color value so as to match the live corals, stocked with newly collected crabs of the proper genera, and placed back in the Eniwetok Island pool. Controls were used as in Experiment 1. After three days the stained acroporid heads lacked the *Tetralia* crabs and the pocilloporid heads lacked the *Trapezia* specimens, though some galatheid crabs and a few shrimps had taken up residence. All but one of the control crabs were found on their respective corals.

The results of Experiments 1 and 2 suggest that size-space relationship (which is the same in dead and live coral) is not an exclusive factor. Also, the oceanographic conditions of currents, wave action, water temperature, and dissolved oxygen were constant in the environment of the live and dead corals, and thus oceanographic factors and the availability of water-borne food were not exclusively responsible for the commensal association. Any of these, or other, factors could be critical in the distribution of these crabs, but the requisite of live coral appeared to be important.

To check this premise, selective collections of corals (Experiments 3-5) were made on the outer reef at the north end of Eniwetok Island. *Pocillopora danae* heads were obtained just inside the algal ridge where this coral abounds. Six buckets of completely dead coral heads of this species (Experiment 3, station 58) were collected from situations that were totally isolated from living corals. These corals yielded 16 species of crabs (to be described in another paper), but contained no specimens of *Trapezia* or *Tetralia*.

Next, live heads of *Pocillopora danae* which were partially dead and overgrown with algae, were processed as follows: Each head was snapped loose from the reef flat with a geologist's hammer and instantly lifted from the water and cleaved. The live portion with small areas of dead coral (Experiment 4, station 59 from which 14 species of crabs were obtained) was placed in one bucket, the totally dead portion (Experiment 5, station 60 with 18 species

of crabs) was placed in another bucket. This process was completed swiftly so as to prevent crab movement from one part of the head to another. Both the live and dead portions of coral included specimens of *Trapezia*.

Thus, Experiments 3, 4, and 5 suggest that *Trapezia* will dwell in dead Pocilloporidae only if a live portion is present, again suggesting that live corals are essential for the commensal relationship. Furthermore, totally live heads of Pocilloporidae (Experiment 6, station 63) yielded 17 species of crabs including 5 species of *Trapezia*, as would be expected from Garth's account and from the control results of Experiments 1 and 2.

Acroporid and pocilloporid coral heads are often found side by side in a given habitat, together with their commensals, *Tetralia* and *Trapezia*, respectively. The very low incidence of mismatched crabs and corals recorded at the time of our experimentation (one record of *Tetralia* on a pocilloporid coral, Garth, 1964: 142) prompted further field studies to determine if these crab genera display a true specificity for their coral families. Live acroporid and pocilloporid corals were collected (Experiment 7), their crabs were exchanged (*Tetralia* placed on Pocilloporidae and *Trapezia* on Acroporidae), and then were placed back in the deep reef pool. After 3 days the crabs were absent, suggesting that a true specificity does exist.

The feeding habits of the Trapeziinae were checked in the laboratory on captive animals used in reproductive studies. Attempts to serve as food either cut fish or algae proved unsuccessful for maintaining breeding animals. Brine shrimp (*Artemia*) nauplii were offered to the crabs with only apparent good results. Experimentally, however, crabs were starved 3 days in clean aquaria (Experiment 8) and then offered tremendous numbers of live *Artemia* nauplii for filter feeding. Half of these crabs were fed at night, the other half during the daytime. After a suitable feeding period had passed, the crabs were killed and the stomach contents examined. In no instance could *Artemia* nauplii, or their fragments, or other plankton, be recognized. On the other hand, *Artemia* eggs, which happened to be introduced with the nauplii and which sank to the bottom of the aquaria, were found in the stomachs of two

specimens of *Trapezia*. These experiments indicate that normal filtered food, meat baits, and algae are not the normal diet of the Trapeziinae.

Next (Experiment 9), crabs were collected in the field from their coral hosts, killed by cutting the carapace (to insure quick preservation), and dropped into solutions of 5% formalin or 75% alcohol. Under microscopic examination (430 diameters), without stain, no specimens of phytoplankton or zooplankton could be recognized. Instead, small round globules of some sort were present in the stomachs. This material was not identified or classified.

Concurrently, a series of laboratory experiments (Experiments 10–13) were initiated to gain better insight into the possible host-specificity exhibited by the Trapeziinae, and to determine the nature of their feeding habits.

For Experiment 10, two aquaria measuring 10 by 24 inches, by 18 inches deep, were set up and supplied with running seawater. Each tank was devoid of foreign material but was provided with one live pocilloporid head with three *Tetralia* and one live acroporid head with three *Trapezia* (these crabs were switched from their "preferred hosts"). The two coral heads in each aquarium were placed about 10 inches apart. After 24 hours the collective results from the two tanks showed that three *Tetralia* had migrated to acroporid coral, one remained on a pocilloporid coral, one was dead and the last was missing; all six of the *Trapezia* had moved to pocilloporid corals. This experiment demonstrated a distinct preference on the part of these crabs to seek out their preferred host coral. The data are not conclusive, but may suggest that this preference is slightly stronger in the *Trapezia* genus.

Experiment 11 utilized two identical running-seawater aquaria devoid of all foreign material. A small head of acroporid coral with five *Trapezia* was placed in one tank, while a pocilloporid coral with five *Tetralia* was placed in the second tank. No other corals were available to these crabs. After 24 hours five *Trapezia* remained on the acroporid coral (although one was dead); four *Tetralia* remained on the pocilloporid coral while a fifth crab (dead) was found a few inches away. These results tend to suggest that physical protection was sought here in the "wrong" coral since the proper

coral was not available. Since the writer can distinguish between most live acroporid and pocilloporid corals on the basis of odor alone, he assumes here that chemical "odor," or the absence of it, may cause these crabs to seek out their preferred host corals when they are present.

Experiment 12 repeated Experiment 10 but arranged the corals in a definite upstream-downstream relationship within the four running-seawater aquaria used. Each of the four aquaria had one acroporid coral with 4 *Trapezia* (a total of 16 *Trapezia*), and one pocilloporid coral with 4 *Tetralia* (a total of 16 *Tetralia*). Corals were placed about 10 inches apart (between the nearest opposing borders). In aquaria A and B the acroporid corals were placed upstream to the pocilloporid corals. The converse was true with aquaria C and D.

The results of Experiment 12 A and B, after 24 hours were as follows: 6 *Trapezia* moved upstream to their preferred pocilloporid corals, while 2 *Trapezia* remained on or under the acroporid coral; 4 *Tetralia* migrated downstream to their preferred acroporid corals, while 4 were missing altogether.

The results, of experiment 12 C and D, after 24 hours were as follows: only 2 *Trapezia* migrated downstream to the pocilloporid corals, while 6 remained on or under the acroporid coral; 4 *Tetralia* migrated upstream to the preferred acroporid coral, 2 remained with the pocilloporid coral, and 2 were lost.

The combined results of experiment 12 show that, of the 16 crabs that did migrate, 10 moved upstream to their preferred host while 6 migrated downstream. Again, these results are not conclusive but suggest that chemical odors may enhance the location of the preferred coral host.

In Experiment 13, 3 *Tetralia* specimens were placed in each of four large running-seawater aquaria which also contained some nylon mesh netting soaked with mucus from live acroporid coral. Only 4 of the 12 test animals located the mucus-gauze "bait" after 24 hours. These experiments were considered incomplete, however, and will be continued in the future.

To test more fully the reactions of *Trapezia* (Experiment 14, using *T. f. ferruginea* and *T. f. areolata*) in its host coral *Pocillopora*, crab

specimens were starved for 3 days, then returned to live corals in small aquaria. When accustomed to the aquaria many crabs began what turned out to be feeding activities. The following is an account of the typical behavior displayed:

The crab climbed into the coral branches, then placed the dactyli of the walking legs (WL) 3 and 4 into polyp cups, depressing the polyps. Next, WL-1 were inserted into other polyp cups between the tentacles of the polyp, and "scratched" back and forth at a rate of about 4 strokes per second, for about 4 seconds. The tips of WL-1 were then alternately cleaned by the mouthparts of the crab. During the cleaning operation, WL-2 were used to scratch new polyps, then were cleaned by the mouthparts. Muroid material could be seen clinging to the tips of the walking legs during this procedure.

Periodically material was transferred from WL-3 or 4 to WL-2 or 1, and then brought to the mouth. Occasionally the chelipeds were moved over the coral epidermis between the polyps. The fingers subsequently were cleaned in the mouthparts of the crab. These activities were repeated over and over again, as the crab slowly moved up through the coral branches.

Upon examining the dactyli of *Trapezia f. ferruginea*, it was noted that a special brush and comb is present on the terminal segments of each leg (referred to henceforth as the food brush and food comb). The food brushes are situated at the distal end of each dactylus (Fig. 1E) and consist of several short, stout, blunt-ended spines for agitating the coral polyp, and a dense tuft of bristles for collecting mucus, bacteria, and other debris. The bristle tuft is fully developed in walking leg 1 but is progressively less well represented posteriorly (Fig. 1 A-D). Borradaile (1903:240) figures the terminal spines of *Trapezia f. ferruginea* and suggests that "the remarkable ending of its legs is in some way connected . . ." with its life in the coral. The terminus of each dactylus protrudes ventrally, thus forming a concavity on the ventral surface of the immediate proximal part of the dactylus. The food combs, shown in the posterior view of the left dactyli (Fig. 1 A-D), consists of from 3 to 6 rows of

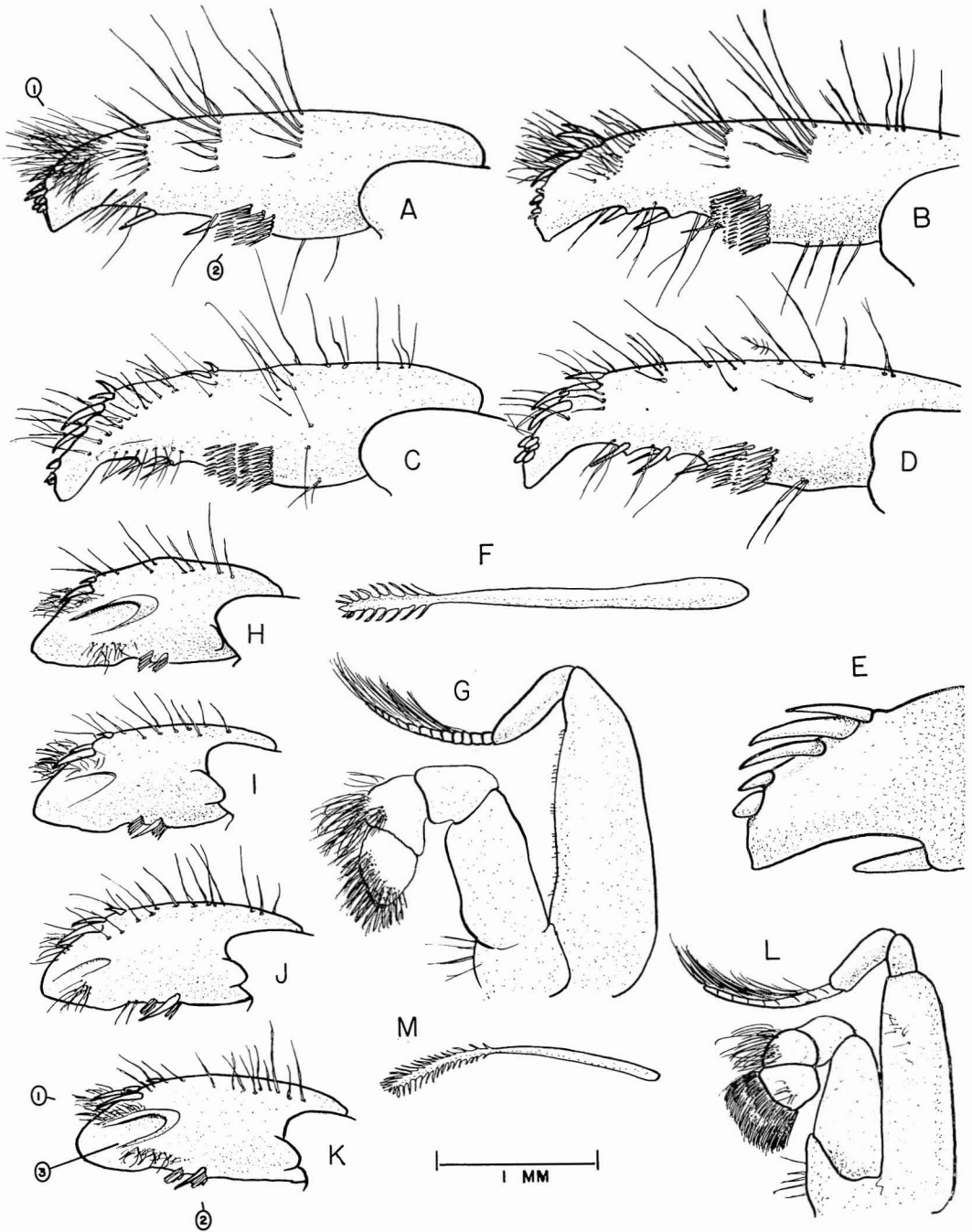


FIG. 1. *Trapezia* f. *ferruginea*: A-D, Dactyli 1-4; E, tip of dactylus 1; F, a bristle from food comb; G, 2nd maxilliped. *Tetralia heterodactyla*: H-K, Dactyli 1-4; L, 2nd maxilliped; M, a bristle from maxilliped food brush. Anatomy: 1, food brush; 2, food comb; 3, groove. (All drawings to the same scale except E.)

feathered bristles (Fig. 1F) which extend under each dactylus and proceed an equal distance up the anteroventral surface of each dactylus. The combs are well developed and are presumably used in concentrating mucus from other legs, and in transferring mucus to other legs or to the mouthparts as described above. The endopodites of maxillipeds 3 are usually well bristled, and those of maxillipeds 2 have a fan of spines and dense tufts of bristles (Fig. 1G) for combing food into the mouth (these are to be known as maxilliped food brushes). Furthermore, the longitudinally bifurcated basal exopodite segment of maxillipeds 1 of *Trapezia* may have a valve function to prevent the loss of food during food-transfer operations.

The dactyli of *Tetralia heterodactyla* (Fig. 1H-K) have relatively small food brushes which are almost equally developed on all legs. The ventral concavity is very shallow and contains two rows of food combs consisting of flat, blunt, unfeathered bristles. These combs are almost restricted to the ventral surface of the dactylus. A conspicuous groove is also present, proximal to the end of each dactylus. These grooves are better developed on WL-1 and 4. The maxilliped food brushes of *Tetralia* are very well developed only on maxillipeds 2 (Fig. 1L), and consist of dense masses of bristles which are feathered (Fig. 1M) distally. The basal segment of the exopodite of maxillipeds 1 are also bifurcated as described for *Trapezia*.

Live corals, in seawater, were examined under a dissecting microscope (Experiment 15), then "scratched" as described for *Trapezia*, with a dull probe. The probe was repeatedly coated with mucus and debris from the coral animal. When examined at 430 diameters, this material proved to be identical with that material on the crabs' food brushes (Experiment 14) and with material in the stomachs of newly-killed and also field-preserved specimens.

These experiments demonstrate that *Trapezia f. ferruginea* is actually a parasite with a strong host specificity, at least on the coral family level. The presence of food brushes on other Eniwetok *Trapezia* species and on *Tetralia* species warrants recognizing them as parasites. The use of the food brushes in feeding would also explain why *Artemia* eggs were found in

the stomachs of crabs offered *Artemia* nauplii for filter feeding. Presumably the eggs were transferred from the aquarium floor to the crabs' mouthparts after they had been picked up on the food brushes.

In a search of the literature for similar coral parasites, Gerlach's paper (1961:3) describes "an as yet unidentified aberrant copepod with a worm-like body which apparently lives on coral, mainly Pocilloporidae These animals could be observed as they crawled about on the surface of the coral and slashed at the tissues of the coral polyps with the sharp claws of the first pair of legs. Here the point to be considered is that this is a form which has become particularly adapted to a mode of life parasitic on coral." This behavior parallels the behavior of Trapeziinae described herein.

As to the degree of parasitism, that is, the effect of the crabs' parasitism upon pocilloporid corals, no data are available. The parasites are probably quite efficient, that is, they do not quickly kill or greatly harm their host. Otherwise, every case where numerous crabs are found occupying a coral head would result in the rapid destruction of the crabs' microhabitat. The amount of food produced for crab consumption (or the number of polyps per head) probably serves as a basis for territoriality observed by Garth (1964:142).

The coral-host preference of the two genera of crabs may well be correlated with the relative difference in size, and thus efficiency, of the food brushes and combs. This conclusion is based on the fact that when live acroporid corals are removed from seawater and placed in the shade they secrete vast quantities of mucus, while pocilloporid corals secrete little mucus under the same condition. *Tetralia*, with the smaller and less efficient brushes and combs, thus takes advantage of a coral family which presumably is capable of secreting the greatest amount of mucus. *Trapezia*, on the other hand, has larger brushes and combs but lives with a less "productive" coral family. More research is being done on this aspect.

The exact basis of the host specificity displayed by these genera of crabs may well be related to the crab-size coral-space premise suggested by Garth, or to the distinct difference in the chemical odor and probable chemical

makeup of the chief source of food, that is, the mucus secreted by the coral animals. In our collections at Eniwetok Marine Laboratory we isolated a large number of corals by species and carefully separated the parasitic and commensal crabs found therein. The identification of these animals may well reveal a more definite species-to-species relationship between crabs and corals. These data and others will be recorded in another paper, along with additional experimentation to be conducted at the Eniwetok Marine Biological Laboratory.

CONCLUSIONS

The literature, our field collections, and field experimentation confirmed that an obligate host specificity exists between the crab genus *Trapezia* and Pocilloporidae corals, and between the crab genus *Tetralia* and Acroporidae corals. Furthermore, these crabs require living corals as a source of food, in addition to protection, and should be recognized as obligate ectoparasites of their respective host corals. There may be a relationship between the food brush and comb size and the apparent ability of the two coral families to secrete mucus which governs the host preference displayed by *Trapezia* and *Tetralia*.

ACKNOWLEDGMENTS

The writer is indebted to the National Science Foundation and to Dr. Robert Hiatt, Director of the Eniwetok Marine Biological Laboratory, sponsored by the Atomic Energy

Commission, for support and assistance; to Dr. John S. Garth, who worked long hours to help review and identify Eniwetok crab specimens; and to my students, Jack Shannon and Dave Pearson, who diligently aided in our field research.

REFERENCES

- BORRADAILE, L. A. 1903. Marine Crustaceans. III. The Xanthidae and some other crabs. In: J. Stanley Gardiner, The Fauna and Geography of the Maldive and Laccadive Archipelagoes 1(3):237-271.
- CRANE, J. 1947. Eastern Pacific Expeditions of the New York Zoological Society. XXXVIII. Intertidal brachygnathous crabs from the west coast of tropical America, with special reference to ecology. Zoologica N. Y. 32(2):69-96.
- GARTH, J. S. 1964. The Crustacea Decapoda (Brachyura and Anomura) of Eniwetok Atoll, Marshall Islands, with special reference to the obligate commensals of branching corals. Micronesica 1(1-2):137-144.
- GERLACH, S. A. 1961. The Tropical Coral Reef as a Biotope. Atoll Research Bull., Pt. 80, pp. 1-6.
- MIYAKE, S. 1939. Notes on Crustacea Brachyura collected by Professor Teiso Esaki's Micronesia Expeditions of 1937-1938, together with a check list of Micronesian Brachyura. Rec. Oceanogr. Work Japan 10(2):168-247.